Coral Recruitment and Sedimentation in Asan Bay and War in the Pacific NHP, Guam

Report prepared for the National Park Service

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Cover Photograph: A coral recruit of the family Pocilloporidae, collected on a recruitment plate from Asan Bay, Guam and War in the Pacific NHP.

Abstract

War in the Pacific NHP has over 400 hectares (1000 acres) of Indo-Pacific coral reefs within its authorized boundary. The reefs are heavily impacted by numerous terrestrial activities. Sedimentation from upland poor land management practices is one of the most significant threats to the long-term health and persistence of the park reefs. Sediments are known to adversely impact coral larvae and juveniles and can impeded successfully settlement and recruitment. Recruitment was monitored in Asan Bay along a sediment gradient using PVC plates to determine baseline levels and to investigate a possible correlation between sediment load and recruitment rate and composition. Plates were deployed for 3 month intervals for 1 year to examine temporal trends. Settlement in the park was found to be very low; only 16 recruits were collected over the course of this project, with *Pocillopora* sp. recruits as the most common. Recruits from the family Poritidae and Acroporidae were also collected. No correlation between recruit density and sediment collection rate was observed, but settlement patterns of recruits on plates suggested light, not sediments (directly) or predation, was the primary factor affecting settlement patterns on the reef. Low recruitment rates, coupled with lower light availability as a result of sediment loads raises significant concerns about the long-term health and persistence of the coral reefs within the park.

Introduction

Coral reefs are important ecological, cultural and economic resources. Over the last 30 years, conditions on many reefs have deteriorated and an estimated 20% of all coral reefs have been effectively destroyed and another 50% are under risk of collapse (Wilkinson 2004) as a result of human activity.

Conservation of these critical resources must begin with an understanding of important demographic processes, including successful recruitment of juvenile corals to the reef. Coral larvae generally spend days to months in the plankton (Harrison and Wallace 1990) before settling as, therefore the adults on a specific reef may not have been source of the reef's larval stock. Management of adult populations may not be the most critical need to ensure long-term persistence of specific coral reefs, and managing for important demographic processes is a more effective strategy for conserving coral reef ecosystems (Hughes et al. 1999, Sale 1999),

Coral larvae and recruits are particularly susceptible to environmental degradation (Richmond 1997). Sedimentation, eutrophication, and contamination from waterborne toxins are stressors that can interfere with or inhibit reproductive processes such as gamete production, release, viability, larval survival, settlement, and ultimately recruitment (Tomascik 1991, Richmond 1993, 1997, Kojis and Quinn 1994; War and Harrison 1997; Harrison 2000; Koop et al. 2001). Concentrations effecting coral larvae and juvenile corals are usually lower than the concentrations that affect adult corals and may be below threshold standards enacted by environmental regulatory agencies.

Asan Bay Guam has approximately 5 km of well-developed fringing reef that lies within the boundary of War in the Pacific National Historical Park. The reef has been heavily impacted from watershed development and terrestrial land practices that have resulted in unnatural fire regimes, accelerated erosion and sedimentation, eutrophication, and pollution.

Sedimentation is the most significant threat to the coral reefs in Asan Bay (Minton 2005). Following even modest rain events, sediment plumes are visible at river inputs along Guam's entire coast. Sediments can kill adult coral colonies by burial, decreasing light penetration, disrupting polyp gas exchange, and inhibiting nutrient acquisition (Rogers 1990, Richmond 1993). Some adult species can be effectively smothered at relatively low sedimentation rates, while others are able to secrete mucous to remove these sediments and are thus more tolerant of elevated sediment inputs (Rogers 1990, Richmond 1993). Even if sedimentation is not visibly impacting adult coral colonies, sedimentation rates may be high enough to inhibit all or some juvenile recruitment (Gilmour 1999, Fabricus and Wolanski 2000).

Elevated sedimentation can cover potential recruitment habitat, intensifying competition for space on the benthos. Although significant interspecific differences exist (Rogers 1990, McClanahan and Obura 1997), heavy sedimentation rates (≥95% coverage of substrate) have been shown to inhibit coral settlement completely, while more moderate rates (≥50%) severely inhibit settlement (Hodgson 1990). Additionally, increased sediment loads seem to disrupt the attachment/metamorphosis process (Hodgson 1990, Gilmour 1999), a critical process for planulae to successfully recruit to the benthos. Since juvenile corals are more susceptible to environmental disturbances, they may be a good indicator of reef health. Conversely, reefs that appear "healthy" may not be receiving sufficient recruits to replace adults, and over time the coral community will deteriorate. This phenomenon has been observed already on some Guam reefs (Richmond 1993, Richmond 1994, Wolanski et al. 2003), raising concern among resource managers about the future, long-term health, and stability of marine resources on Guam.

Soil erosion on Guam is occurring at significant levels (National Resource Conservation Service 1996, Wolanski et al. 2003, Minton 2005) and may be acting as a barrier to coral recruitment, particularly at some locations along the reef at War in the Pacific National Historical Park (Lundgren and Minton 2005). Understanding the relationship between sediment load and coral recruitment is vital to mitigating disturbance and understanding one of the mechanisms that regulate benthic populations and mediate species coexistence on the reef.

The objectives of this study were to: 1) assess spatial and temporal patterns of coral recruitment at War in the Pacific National Historical Park; 2) examine the relationship between the sediment deposition and coral recruitment rates; and 3) provide baseline data on coral recruit taxonomy. With this information, natural resource managers would be able to identify reef areas experiencing sedimentation-related recruitment limitation and develop best management practices for erosion mitigation in the adjacent watershed.

Material and Methods

Study Design

A pilot study was conducted from March-August 2004 to assess the feasibility of settling corals onto experimental plates and to determine the level of taxonomic resolution for recruit identification (Lundgren and Minton 2005). Information from the pilot study was also used to aid in site selection for this project. Data and logistical insight derived from two 3-month deployments of recruitment plates indicated that working at a single depth, using paired sites would diminish possible confounding variables (i.e. coral cover, species richness, wave action, temperature, and salinity). Additionally, data from a yearlong sedimentation baseline study (Minton 2005) provided sufficient data to allow selection of paired sites approximately 150 m apart (Figure 1) that experienced elevated and moderately elevated sediments loads. The close proximity of these paired sites reduced the likelihood of confounding variables affecting the project's results. All selected sites were at 20 meters depth on the fore reef slope and were a subset of those included in the sediment projects described by Minton (2005) and Minton et al. (2005).

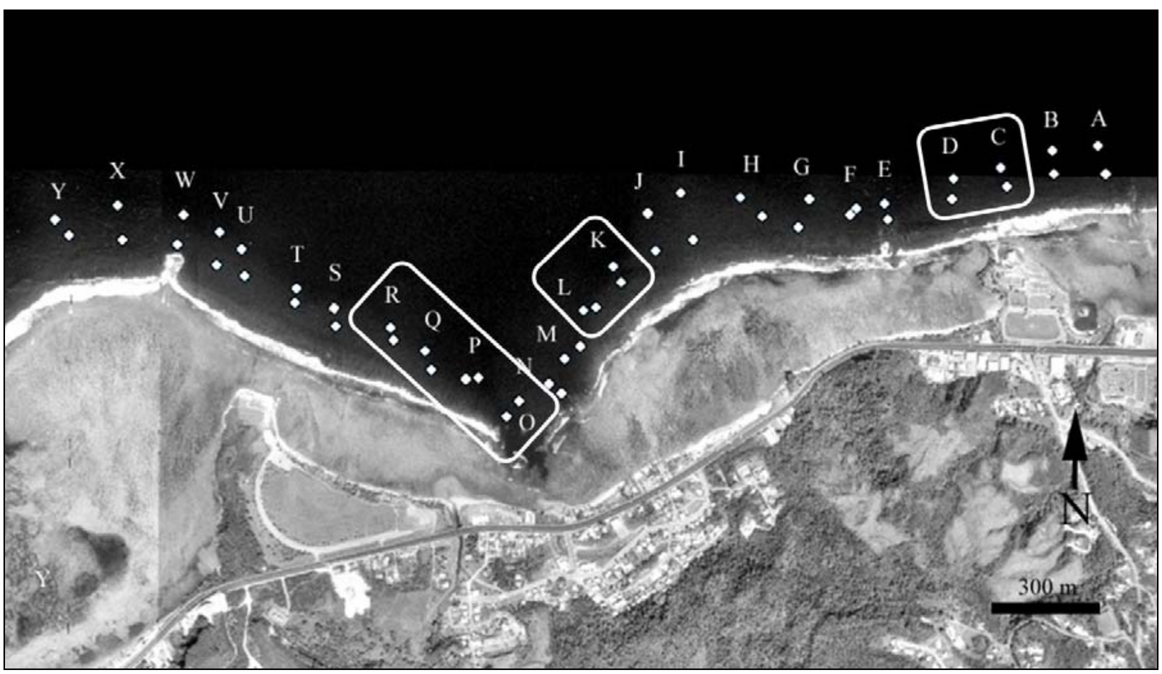

Figure 1. Coral recruitment arrays were deployed at eight study sites in Asan Bay, Guam. Study sites were a subset of locations where the War in the Pacific NHP has conducted two years of sediment monitoring. Each lettered sediment site was comprised of two sediment collectors, one placed at 10 m and second at 20 m. Coral recruitment arrays were placed only at the deep water locations (C20, D20, K20, L20, O20, P20, Q20, and R20).

Methods

At each of the eight study sites three recruitment plate arrays (Figure 2) were attached directly to the benthos using "all thread" posts. Each array consisted of four 15x15 cm PVC plates arranged in two stacks of two plates separated by a 10 mm gap using rubber washers. The plates were drilled through the center and held together using stainless steel bolts, washers, and wing nuts. Stacks were braced using three Plexiglas strips, which could be attached to the posts and secured with a short section of tubing and a hose clamp. To ensure uniform orientation and elevation with respect to the benthos, a small spacer was placed underneath the array that held it approximately 5 cm perpendicular to the benthos. Each recruit array had 782.25 cm^2 of plate space available for settlement.

By placing the tiles in stacked pairs, four distinct plate surfaces were created, each with a unique combination of sediments, predation, and light availability (Table 1). The upper surfaces of the plates were exposed to sediments and sunlight, whereas lower surfaces did not collect sedimentation and were shaded. The two surfaces in the middle of the stack (top plate lower surface and bottom plate, upper surface) – hereafter, "gap" surfaces – were exposed to lower grazing pressure. The other surfaces were accessible to small parrotfish, echinoderms and large grazing mollusks.

Three sampling arrays were deployed at eight sites in Asan Bay, Guam (Figure 1), within the boundary of War in the Pacific NHP. Sampling arrays were placed approximately 5 meters upstream, downstream, and shoreward of a sediment sampling array. Plates were

Figure 2. Coral recruitment array deployed on the bottom.

Table 1. Sedimentation, predation, and light conditions on the four plate surfaces present in the coral recruitment sampling arrays.

Plate	Surface	Sedimentation	Predation	Light
Top	Upper	High	High	High
	Lower	Low	Low	Low
Bottom	Upper	High	Low	Moderate
	Lower	Low	High	Low

deployed for consecutive three-month periods from October 2004-October 2005, collected and transported to a wet lab. All plates were handling by the edges and transported so that their settlement surfaces were not damaged. At the wet lab, plates were unassembled, labeled and high-resolution digital photographs (5 megapixel) were taken while organisms were immersed and fresh to record community composition for possible future analysis. Plates were then bleached. Algal material was carefully removed while searching for recruits under a dissecting microscope. All recruits were identified to the lowest possible taxonomic level, generally family, following Babcock at al. (2002). High-resolution digital photographs of each recruit were taken using a dissecting microscope fitted a MaxView Plus adapter set and an Olympus 5050 digital camera.

Sediment sampling arrays and sediment methodologies were identical to those employed by Minton (2005). Briefly, three PVC tubes were assembled into a single sediment array and deployed on the reef for consecutive three week periods. Tubes were capped *in situ* and returned to the lab, where two tubes were processed for total sediment dry weight, percent organic material, and percent $CaCO_3$. The third tube was processed for grain size. All data was stored in a Microsoft Access database. At each recruitment site, over two years of continuous sediment data has been collected, much of which has been analyzed elsewhere (Minton 2005; Minton et al. 2005).

Temperature data loggers (Onset HoboTemp) were deployed at each site. Two CTD units (Star-Oddi DST CTD data logger) were rotated among sites every three weeks to obtain salinity, tidal, and temperature data. Daily weather and rainfall data were obtained from the National Weather Service at Tiyan, Guam.

Plate and surface preferences were compared to random using a Chi-square test for goodness of fit. Few recruits were observed over the course of the study, so sediment effects could not be examined using paired methods. Sediment data at one site during one replicate was lost, so sediment data was analyzed for spatial and temporal differences using a reduced model ANOVA. Logistic regression was used to examine the relationship of recruits to sediments (Sokal and Rolff 1995). Presence or absence of recruits at the site was the response variable with sediment collection rate ($g/cm^2/day$) as the predictor variable. A G-statistic was calculated to test for significance. Goodness of fit was fit was examined using Pearson and Hosmer-Lemeshow statistics as well as examination of leverage values. Minitab statistical software was used to conduct all statistical analyses.

Results

Only 16 coral recruits were observed on 384 plates totaling 30.04 m^2 (Appendix A-C), equating to a mean (±SE) of 0.021±0.001 recruits/plate surface or 1.07±0.31 recruits/m^2 in Asan Bay. Recruits belonged to three taxonomic families: Pocilloporidae (10 recruits), Poritidae (5 recruits), and Acroporidae (1 recruit). Further taxonomic resolution could not be obtained, as identification of juvenile recruits beyond the family or generic level is problematic. However, all of the pocilloporid recruits were most likely the brooding coral *Pocillopora damicornis*.

Using size and morphological characters as described in Babcock et al. (2003), individual recruits appeared to vary in age from a few days to several months. For example, recruit 1-D20 (Appendix B) was comprised of a single corallite, whereas recruit 1-O20 was composed of at least 12 corallites. Only pocilloporids were observed to have more than a single corallite deposited on the plate; all poritid and acroporid individuals consisted of a single coral polyp.

Coral recruits were not randomly distributed on the four plate surfaces (Chi-square test; X^2=18.5; df=1; p<0.0001). Coral recruits settled more than expected on the upper surfaces of plates (Table 2), where 11 of 16 recruits were found. Only 1 of 16 recruits was observed on the underside of a plate (site D20, replicate 3). Gap surfaces (top plate, lower surface, and bottom plate upper surface) had moderate recruitment (4 of 16), but this value did not vary from that expected with random settlement.

Coral recruit distance from the edge of plate did not vary between the upper surfaces of the top and bottom plate (Mann-Whitney; W=93; df; p=0.56), but sample sizes were very small. In general the recruits on the bottom plate were closer to the edge (median=4mm), while recruits on the top plate were farther from the edge (median=12mm) and more widely distributed over the plate (Figure 3, Appendix B).

Table 2. Distribution and identity of coral recruits on plate surfaces. Distribution of coral recruits is not random (Chi-square test; X^2=18.5; df=1; p<0.0001). Acrop=Acropoidae; Pocil=Pocilloporidae, Porit=Poritidae.

	Upper Surface	Lower Surface
Top Plate	11 (Acrop, Pocil x7, Porit x3)	0
Bottom Plate	4 (Pocil x3, Porit)	1 (Porit)

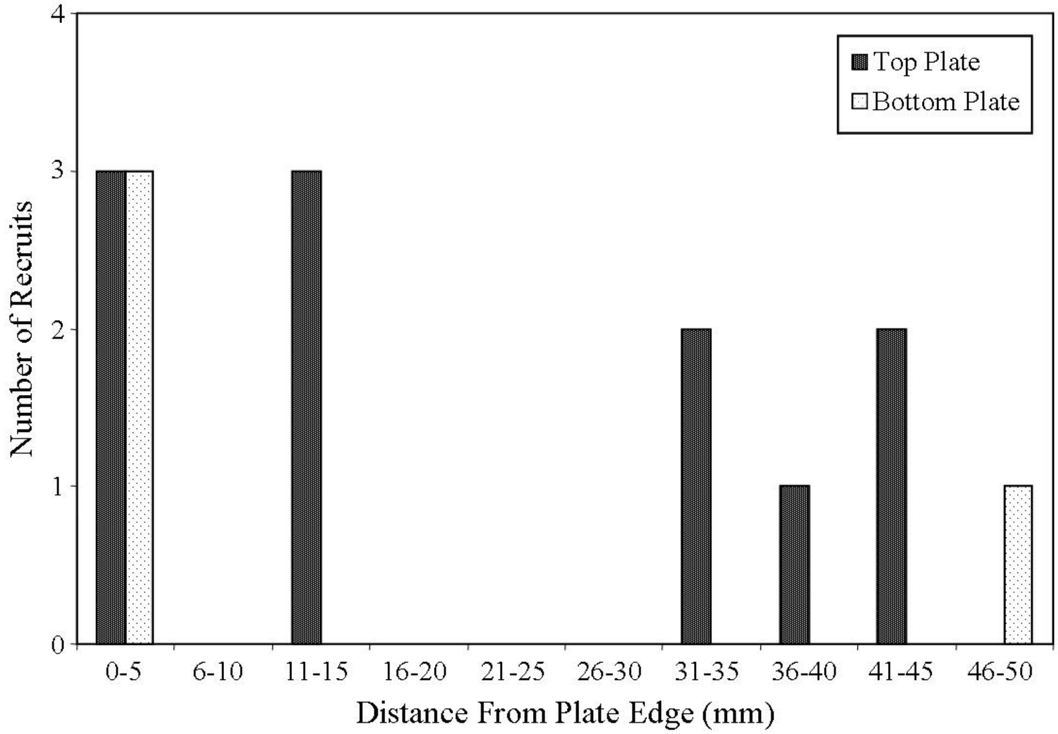

Figure 3. Distance of coral recruits from the edge of top and bottom plates. All data is for the upper surfaces of the plate.

The low numbers of coral recruits did not allow for statistical examination of within-site spatial variability. Recruits were found at all sites except R20. Variability across-sites is low (Table 3) and does not appear to be related to within-site characteristics, such as coral cover. Sites ranged in coral cover from approximately 5-60% coral cover, with sites C20 and D20 having the highest cover and sites K20 and L20 the lowest (per. obs.).

Table 3. Number and identity of coral recruits collected at eights sites in Asan Bay and War in the Pacific NHP.

Location	Recruits	Identity
C20	1	Poritidae
D20	4	Pocilloporidae (x3), Poritidae
K20	3	Pocilloporidae (x2), Poritidae
L20	2	Pocilloporidae (x2)
O20	2	Pocilloporidae (x2)
P20	3	Poritidae (x2), Acroporidae
Q20	1	Pocilloporidae
R20	0	

Seasonal trends are difficult to discern with only one year of data. The peak in coral recruitment occurred during the coral spawning (Replicate 4), which, on Guam, occurs 7-10 days after the full moon in June (June 22, 2005), July (July 21, 2005), and August

(August 19, 2005). Taxonomic diversity was also highest during Replicate 4 (Table 4). The Pocilloporidae recruited year round in fairly constant numbers, suggesting that these are a brooding coral species, the most likely candidate being *Pocillopora damicornis*. This species is present in the study area, is known to brood on Guam (Richmond and Hunter 1990), and the recruits had skeletal characteristics consistent with those described for the species (Baird and Babcock 2000; Babcock et al. 2003). The poritid recruit may also represent a brooding species (Andrew Baird, personal communication). Of the acroporids with which information about their reproductive mode is known for Guam, approximately 20% are brooders (Richmond and Hunter 1990).

Table 4. Number and identity of coral recruits collected in each study replicate.

Replicate	Date	Recruits	Identity
1	Oct 2004-Jan 2005	3	Pocilloporidae (x3)
2	Jan-April 2005	4	Pocilloporidae (4)
3	April-June 2005	2	Poritidae (x2)
4	June-Sept 2005	7	Pocilloporidae (x3), Poritidae (x3), Acroporidae

Site O20 had significantly higher sediment collection rates than all other sites except for P20 (ANOVA; $F=4.25$; $df=7,22$; $p=0.005$). Other sites did not significantly vary in their sediment collection rate. Sediments did not vary among replicates (ANOVA; $F=2.31$; $df=3,22$; $p=0.107$).

Coral recruitment was independent of sediment collection rates (Logistic Regression; $G=3.12$; $df=1$; $p=0.077$). Interestingly, the slope of the regression line, while not significantly different from zero, was positive, suggesting a positive relationship between recruitment and sedimentation. This was the result of consistent recruitment at site O20, which also had the highest sediment collection rates (Appendix A). In particular, two values at O20, sediment collections rates of 0.1686 (Replicate 1) and 0.2345 g/cm2/day (Replicate 2) had very high leverage values.

Discussion

Compared other coral reefs areas, the recruitment rates measured in Asan Bay, Guam (0.021 recruits/plate or 1 recruit/m^2) are among the lowest in the world. These low recruitment rates do not appear to be unusual for the Mariana Islands, where rates are consistently several orders of magnitude lower than other areas (Table 5). Direct comparison of different studies is problematic; recruitment can significantly vary with plate material (Harriott and Fisk 1987, Reyes and Yap 2001), depth (Birekland et al. 1981), and deployment time (Birkeland et al.1981). However, in a study using similar methodology at each site, Kojis and Quinn found rates in the Northern Mariana Island (CNMI 24 recruits/m^2: Rota=0 recruits/m^2; Tinian=22.5 recruits/m^2; Saipan=49.3 recruits/m^2) to be an order of magnitude lower than in the Virgin Islands (134 recruits/m^2) and Fiji (734 recruits/m^2). They attributed the low recruitment rates in the Mariana Islands to poor larval supply (Kojis and Quinn 2001).

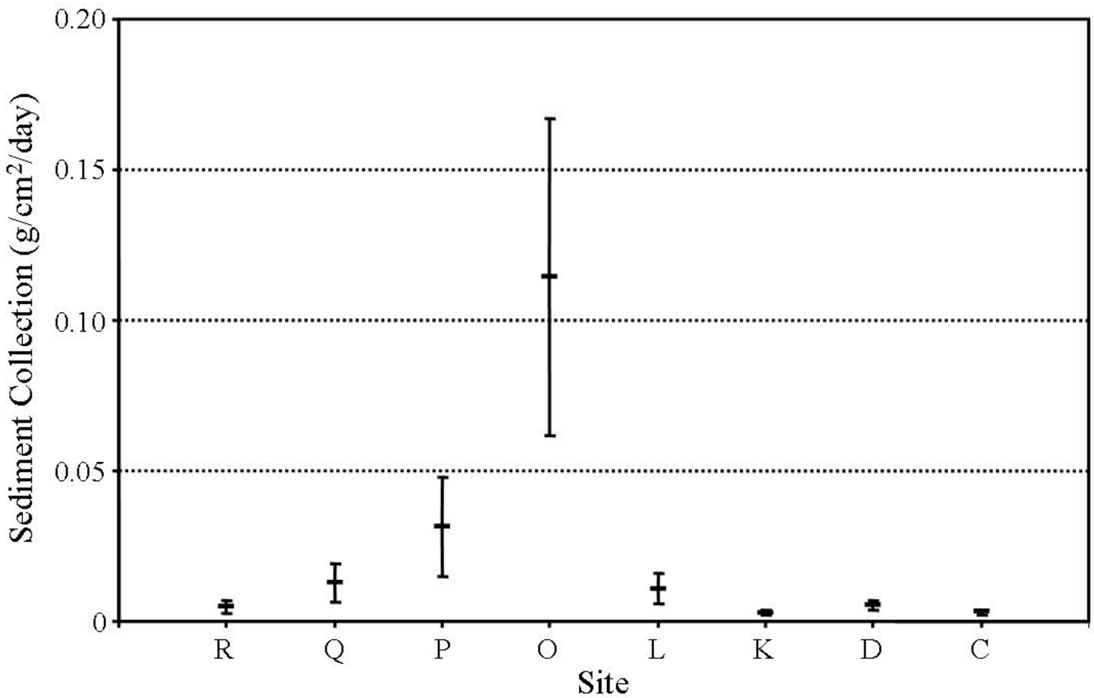

Figure 4. Sediment collection rates at 8 sites in Asan Bay from October 2004-2005. Sites correspond to those in Figure 1. Points are the mean (±SE) sediment collection rate for four three-month long replicates, except for site C where data for replicate 3 was lost.

On Guam, Birkeland and others (1981), using nearly identical methods to those in this study, found 23 coral recruits on 158 plate surfaces (0.146 recruits/plate surface) deployed for 100 days, compared to 16 recruits on 768 plate surfaces (0.021 recruits/plate surface) deployed in this study for a similar time period. This trend in declining recruitment on Guam has been observed by others. Birkeland repeated his earlier work at in 1989 and 1991 (Birkeland and Sakai in Birkland 1997) and collected only 2 recruits on 936 plate surfaces (0.002 recruits/plate surface), compared to 278 recruits on 1050 total plates surfaces (0.265 recruits/plate surface) in 1978. At Tanguisson, Guam, 112 recruits were collected on 564 plate surfaces (0.20 recruits/plate surface) in 1981 (Neudecker 1981). In 1992 only 2 recruits on 448 plate surfaces (0.004 recruits/plate surface) were found at the same location (Chirichetti in Birkeland 1997).

While post-settlement factors cannot be entirely ruled out as possible explanations for the observed recruitment patterns in Asan Bay, the low number of recruits, lack of dead skeletons, and relatively short *in situ* time suggests that pre-settlement factors may provide the best explanation for the observed patterns in this study. Three possible pre-settlement factors, two operating at the local scale (Asan Bay) and one at the regional scale (Island/Indo-Pacific), could explain the recruitment patterns observed in Asan Bay. These factors, which are not mutually exclusive, include:

1. Decreased water and habitat quality in Asan Bay is impairing larval settlement (local scale).
2. Decreased water quality in Asan Bay is reducing the available larval pool (local scale).
3. Fewer larvae are arriving in Asan Bay (regional scale).

Local Scale

The drop in coral recruitment over the last 20-30 years on Guam may be associated with declining water quality and small scale (mm-cm) benthic habitat condition. On Guam, human population increased from 105,979 to 154,805 people between 1980 and 2000 (US Census Bureau 2001). Coastal villages have seen a nearly 25% increase in population during this same time (US Census Bureau 2001). Guam's aging infrastructure and increased coastal development, particularly the expansion and installation of coastal roads and other impervious surfaces, have contributed to numerous environmental impacts on the island's coral reefs (Wolanski et al. 2003; Porter et al 2005). Over the past 25 years, sediment impacts to Guam's coastal ecosystems have increased (NRCS 1996, Birkeland 1997). Coastal golf course development, broken sewage outfall pipes, and an inadequate stormwater system have contributed to elevated nutrients and other contaminants in Guam's nearshore waters (Richmond 1993; Porter et al. 2005).

In Asan Bay, sediments, nutrients, and other contaminants are a significant problem. Sediment collection rates often exceed levels considered detrimental to adult corals (Minton 2005) and may contribute to increased nutrient and bacteria levels. Sediments present in Asan Bay are primarily silts and clays (Minton 2005), which have been shown to be particular detrimental to corals (Fabricius and Wolanski 2000). In 1998, Asan Bay had the fourth highest *enterococci* levels (10.74 cfu/100 ml) among 34 island sites monitored by the EPA (GEPA 1998), and in 2004, water quality advisories were issued for Asan Bay for 37 of the 50 weeks that data was available. Preliminary assessments have detected endocrine disruptors in high levels in both Asan Bay and the adjacent Piti Bay (D. Gochfeld, pers. comm.).

Coral larvae are more susceptible to waterborne pollutants than adults (Richmond 1997), so while water conditions may not adversely affect human health, or even adult corals, they may be lethal to coral larvae and recruits. These impacts have been shown to have direct adverse impacts on Guam's coral fecundity and larval supply (Richmond 1993) and may contribute to changes in the substrata condition through natural eutrophication. Elevated nitrogen levels can affect coral fecundity (Kojis and Quinn 1994; Ward and Harrison 2000), fertilization rates (Koop et al 2001), and settlement (Tomascik 1991; Ward and Harrison 1997). Organisms that respond quickly to altered water quality conditions (e.g. filamentous algae) can monopolize substrata and reduce successful settlement, thus lowering recruitment rates (Birkeland 1977; Rogers et al 1984; Sato 1985; Hunte and Wittenberg 1992; Vermeij 2005).

Table 5. Average recruitment rates (recruits/m^2/ yr) on various artificial substrates in the Caribbean, Pacific, and Indian Oceans. Results for Guam and the Mariana Islands are highlighted.

Site, Island	Ocean	Substrate	Average Recruitment Rate	Latitude	Reference
Great Barrier Reef, Australia	Pacific	Clay	4,258	10-23° N	Hughes et al. (1999)
Cape Tribulation, Australia	Pacific	Ceramic	2,689	14° S	Fisk and Harriott (1990)
Fiji	Pacific	Ceramic	734	17-18° S	Kojis and Quinn (2001)
Zanzibar, Tanzania	Indian	Terracotta	594	6° S	Franklin et al. (1998)
Tanguisson, Guam	Pacific	PVC	530[1]	13° N	Neudecker (1976)
Great Barrier Reef, Australia	Pacific	Ceramic	489	15° S	Fisk and Harriott (1990)
Taa, Tanzania	Indian	Terracotta	282	5° S	Nzali et al. (1998)
Discovery Bay, Jamaica	Caribbean	Coral Slab	251	17° N	Rylaarsdam (1983)
Luminao Beach, Guam	Pacific	PVC	209	13° N	Birkeland (1981)
St. Thomas, Virgin Islands	Caribbean	Ceramic	134	18° N	Kojis and Quinn (2001)
Moorea, Tahiti	Pacific	Ceramic	82	17° S	Gleason (1996)
Guana Island, Virgin Islands	Caribbean	Terracotta	59	18° N	Carlon (2001)
Northern Mariana Islands	Pacific	Ceramic	24	14-15° S	Kojis and Quinn (2001)
St. Croix, Virgin Islands	Caribbean	Coral Slab	6	18° N	Rogers et al. (1984)
Luminao Beach, Guam	Pacific	PVC	2[2]	13° N	Birkeland et al. (1997)
Asan Bay, Guam	Pacific	PVC	1	13° N	Minton and Lundgren, this study

[1]Only control sites were used for rate calculation.
[2]Rate was calculated based on methods described in Birkeland et al. 1981

Coral recruitment patterns are a result of pre-settlement larval habitat selection (Babcock and Mundy 1996; Kuffner 2001; Baird et al. 2003) and post-settlement factors (Sammarco 1981, Sato 1985, Smith 1997). Coral larvae can discriminate between substrata, and tend to show a marked preference for horizontal surfaces, crevices, or the undersides of plates (Birkeland et al. 1981, Rogers et al 1984, Harrison and Wallace 1990).

Coral recruits preferentially recruit to vertical surfaces and plate bottoms when exposed to sediments (Babcock and Davies 1991, Maida et al. 1994, Gilmour 1999). The number of larvae settling on the undersides of plates increases proportionally with sediment load (Babcock and Davies 1991), but may eventually be limited by light availability (Maida et al. 1994). At sufficiently high sediment levels, perhaps when light no longer supports photosynthesis on plate underside or the water is sufficiently turbid to reduce the adverse effects of UV radiation (Kuffner 2001), coral recruits should begin to colonize the upper surfaces of plates (Maida et al 1994), provided they can tolerate the sediment load and any predation effects.

In this study, the observed pattern of plate surface use by recruits is be best explained by light availability and quality, which appears to override sedimentation and/or predation effects on Asan Bay reefs. Most recruits settled on the upper-most surface (top plate, upper surface), where light was presumably the greatest, but also where sediment and predation effects were at their maximum. Light and sediment are not independent factors; as sediment loads increase, light quantity and quality changes. Sediment loads of 100 mg/cm^2 can result in a 75% decrease in ambient light (Riegl and Branch 1995). While not directly quantified here, sediments of 1 mm thick covered more than 50% of the available settlement area (per. obs.) of the upper-most plate surface, a rate that caused recruitment failure in laboratory experiments (Hodgson 1990). Recruit distribution across the upper-most surface was uniform, in contrast to the recruits that settled on the gap surfaces, where recruits tended to cluster along the plate edge, presumably where light levels would be the highest (Mundy and Babcock 1998). Perhaps by placing the recruitment surfaces where light was potentially already limiting (i.e. 20m depth) and effectively forcing recruits onto the most heavily sedimented surfaces, we observed lower recruitment rates than those occurring in shallower water, where a greater number of sheltered microhabitats could be exploited by settling coral larvae.

Post-settlement predation can affect the distribution of coral recruits (Harriot 1985; Sato 1985; Dunstan and Johnson 1998), but the importance of predators on recruit survival is unclear; some studies have shown that scarids will avoid coral recruits and can enhance recruit survival (Birkeland 1977). In this study, the role of predators is equally unclear. Predators were present, as evidence by scarid feeding scars on the plates (Figure 5), but their impact on coral recruits is unknown.

Light limitation, partially related to depth, but more importantly to sedimentation, appears to be the primary environmental factor controlling the settlement patterns of coral recruits in Asan Bay. In combination with sediments, these factors appear to restrict the available settlement habitat and to inhibit larval settlement; together they may partially explain the low recruitment rates within Asan Bay and War in the Pacific NHP.

The sites in this study were on a sediment gradient that covered three orders of magnitude (0.008-0.23 $g/cm^2/day$), yet no significant differences in coral recruitment were observed. Even the minimum sediment collection rate was high compared to many coral reef areas (Minton 2005), and it is possible that all of the study sites had sufficient sediments to impair habitat and water quality and coral recruitment. Data was limited, however, and these results should be interpreted with care.

Low and declining recruitment rates in the Mariana Island and Guam have been attributed to the reduced larval supply (Birkeland et al. 1981, Birkeland 1997; Kojis and Quinn 2000). Birkeland and others (1981) found that plate size did not affect the number of settling coral recruits, suggesting that settlement habitat was not limiting coral recruitment. Indeed, adequate space for larvae to settle was present in this study, but the condition of that habitat was poor.

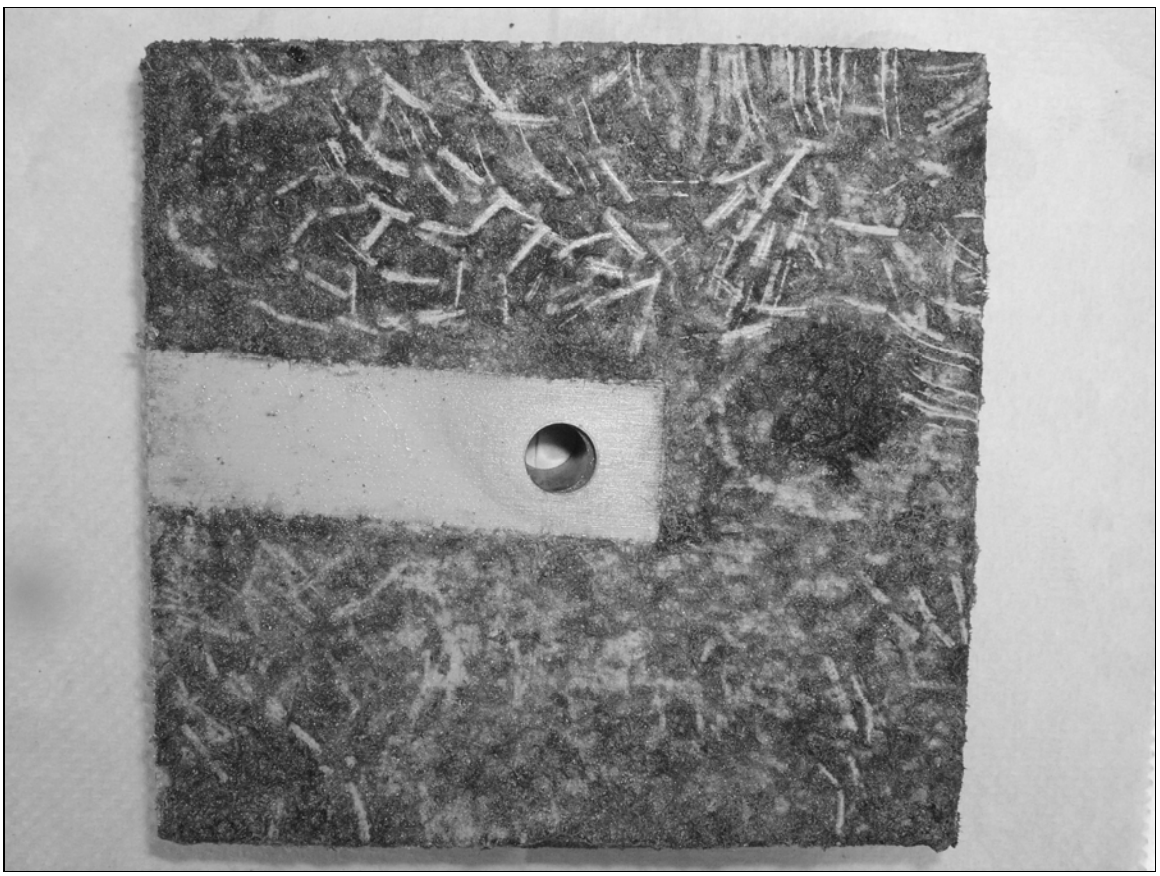

Figure 5. Parrotfish bite scars present of the uppermost plate surface (top plate, upper surface). Clear patch on the plate was not exposed to coral recruitment and was exclude from all calculations.

Sediment laden, freshwater plumes associated with large rain events are frequently observed in Asan Bay, especially during the island's wet season (Minton 2005). Evidence of wet season sediment flushing events, in which unusually large sediment loads are washed from the adjacent watershed on the reef, have been observed at the onset of the wet season (Minton 2005). Many of these plumes can last for several days, floating as a sediment-rich, freshwater surface layer. The timing of this flushing event and the other large plume events corresponds with the island's spawning season (June-August), increasing the risk that coral larvae will be exposed to water conditions that can cause up to 86% mortality of coral larvae (Richmond 1993).

The impact of these stressors on the coral larval supply in Asan Bay is unknown, but poor water quality is a persistent problem and may be destroying the larval stock before it has an opportunity to settle. This may not be restricted to spawning corals. *Pocillopora damicornis* planula do not settle immediately, are positively buoyant and float to the surface (Harii et al. 2002), where it can spend over 100 days before settling (Richmond 1987; Harii et al 2002). Such planular behavior would put this species at risk of encountering adverse surface water conditions in Asan Bay.

Regional Scale

Coral larvae are planktonic and often have long competency times, allowing for long range dispersal. As a result, larval supply may not be a function of the local adult populations (Hughes et al. 2000), but may originate tens to hundreds of kilometers away, depending upon a species' mode of reproduction (brooding vs. spawning) and species-specific larval characteristics. In Asan Bay, the recruitment rate was not related to the local coral cover. Recruits were evenly distributed across eight sites with Asan Bay, regardless of the within site coral abundance.

The origin of Asan Bay's larval stock is unknown. Current patterns around Guam are poorly understood, but preliminary modeling suggests that coral stocks in Asan Bay may originate primarily on Guam (Wolanski et al. 2003). Eddies along Guam's southwest coast may recycle larvae from as far south as Cocos Lagoon, the southern most location on Guam, and bring them into the Asan Bay area (Figure 6). Coastal road construction along Guam's southwest coast in the 1980s has been linked to a massive coral die off (Richmond 1993) that has yet to recover (Wolanski et al. 2003). As a result, the larval stock in Asan Bay maybe lower now than 25 years ago when Birkeland et al. (1981) conducted their work at Luminao Beach (which is also located within southwest Guam gyre).

The current modeling does not adequately capture oceanographic conditions during tropical cyclones or El Niño events (Wolanski et al. 2003). Changes in oceanographic conditions at these times may periodically allow for larvae originating outside of the Mariana Islands to become a significant component of the Guam's larval stock. Processes working at a regional scale or locally in upstream populations, would have direct impacts on Guam's larvae stock.

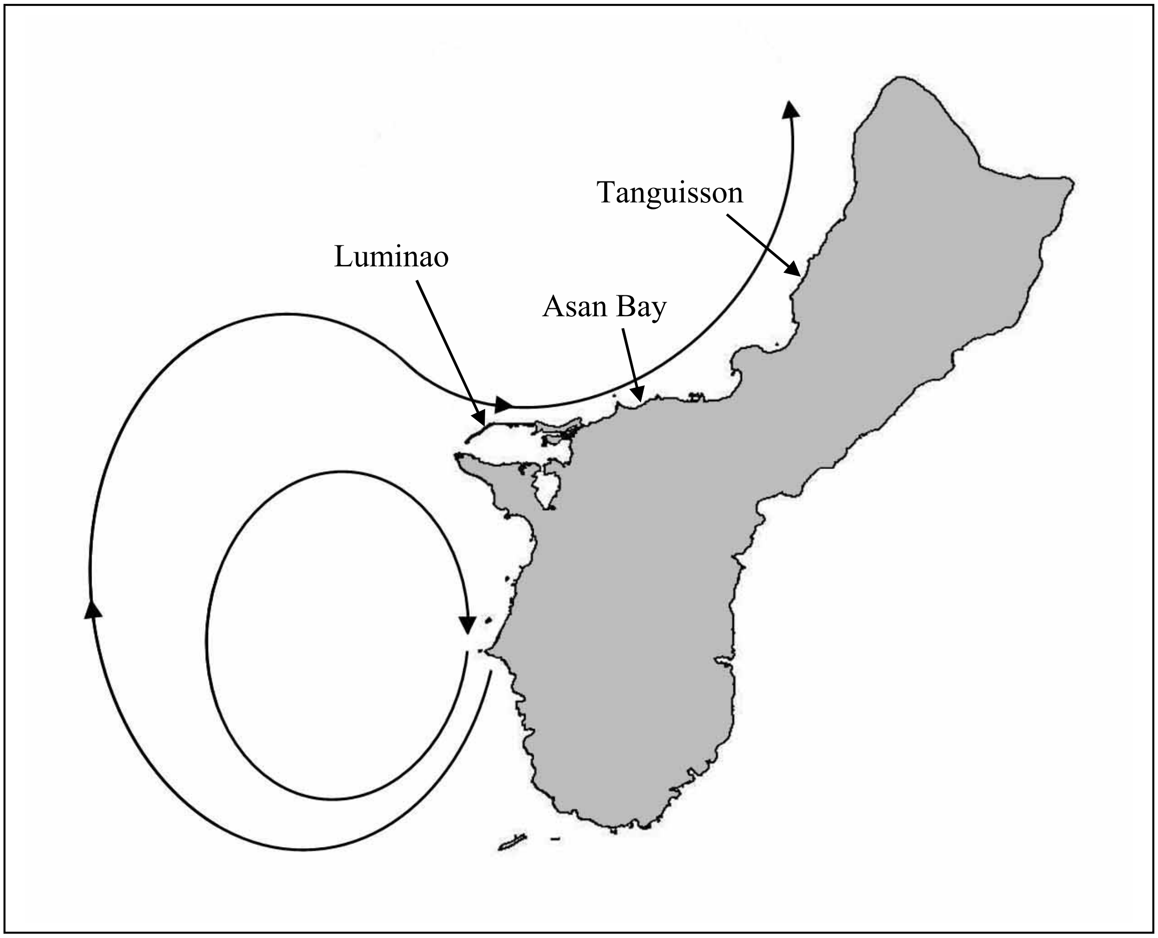

Figure 6. Hypothesized current patterns occurring during a typical northwest far-field current around Guam (adapted from Wolanski et al. 2003).

The condition of coral reefs worldwide has worsened over the past 30 years (Wilkinson 2004). Drops in coral recruitment rates over the last three decades have not been restricted to Guam; Jamaica (Connell et al. 1997), and Curacao (Vermeij, In Press), raising concerns that coral reef health in Asan Bay may be beyond local management efforts.

Management Implications

The success of management efforts to protect coral reefs depends upon a clear understanding of coral reproductive ecology (Hughes et al. 1999, Hughes et al. 2000). In Asan Bay, extant adult populations may be contributing little to the local larval pool, and thus may be disassociated from the future population within the bay. Exclusively, managing the local adult population may be unwise; instead, managing the dynamics of the population, including recruitment, may be the best management approach (Sale 1999).

The results of this study raise serious concerns for the long-term health and persistence of the coral reefs in Asan Bay and at War in the Pacific NHP. Recruitment rates have declined by an order of magnitude in the last quarter century and are now among the lowest rates in the world (Table 5). These declines are probably the result of decreased larval stock and declining environmental conditions within Asan Bay.

It appears that the National Park Service has little ability to enhance its larval supply and should focus on improving local conditions to ensure the highest rate of successful larval survival, settlement and recruitment.

Current conditions in Asan Bay are poor and appear to be inhibiting recruitment. High sediment loads (Minton 2005) and pollution (GEPA 1998, Porter et al. 2005), need to be mitigated with better land management and maintenance of sewage infrastructure. Minton (2005) proposed and examined the feasibility of potential land management activities that could reduce coastal sedimentation. These projects, if successful, would improve coastal water quality and consequently improve the condition of settlement habitat. Better watershed management is needed, and local agencies should address the dearth of watershed management planning sooner, rather than later.

Coral reefs along Guam's southwest coast appear to be the likely source population for Asan Bay's coral larval supply. Efforts should be made by the National Park Service to enhance watershed management in these areas through partnerships with the territorial government, other land management agencies, and private landowners.

While coral cover on Guam has been declining the last 25 years (Birkeland 1997), Asan Bay still contains areas of exceptional coral abundance. The survival rate of adult corals in Asan Bay is unknown, but periodic, extreme events cause mortality. Tropical cyclones in combination with natural senescence and mortality from other factors (e.g., disease, bleaching, crown-of-thorns, etc.) are killing adult corals. If successful recruitment isn't occurring at an equal rate, Asan Bay's reefs will decline. If efforts are not made by resource managers, the local territorial government, and the general public to reverse this trend, Asan Bay's coral reefs may already be dead.

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References

Babcock, R. C., A. H. Baird, S. Piromvaragorn, D. P. Thomson, and B. L. Willis. 2003. Identification of scleractinian coral recruits from Indo-Pacific Reefs. *Zool. Studies* 42: 211-26.

Babcock, R. C. and P. Davies. 1991. Effects of sedimentation on settlement of *Acropora millipora*. *Coral Reefs* 9:205-8.

Babcock, R.C. and C. P. Mundy. 1996. Coral recruitment: consequences of settlement choice for early growth and survivorship of two scleractinians. *J. Exp. Mar. Biol. Ecol.* 206: 179-201

Baird, A. H. and R. C. Babcock. 2000. Morphological differences among three species of newly settled pocilloporid coral recruits. *Coral Reefs* 19:179-83.

Baird, A. H., R. C. Babcock, and C. P. Mundy. 2003. Habitat selection by larvae influences the depth distribution of six common coral species. *Mar. Ecol. Prog. Ser.* 252: 289-293.

Birkeland, C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proc. 4th Int. Coral Reff Symp.* 1:15-21.

Birkeland, C., Rowley, D., Randall, R.H., 1981. Coral recruitment patterns at Guam. *Proc. 4th Int. Coral Reef Symp.* Pp. 339-344.

Birkeland, C. 1997. Status of coral reefs in the Maraianas. In *Status of Coral Reefs in the Pacific* (R. W. Grigg and C. Birkeland, eds.). Sea Grant. Honolulu, HI. Pp 91-100.

Carlon, D.B., 2001. Depth-related patterns of coral recruitment and cryptic suspension-feeding invertebrates on Guana Island, British Virgin Islands. *Bull. Mar. Sci.* 68, 525-541.

Connell, J. H., T. P. Hughes and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment and disturbance at several scales in space and time. *Ecol. Monogr.* 67:461-88.

Dunstan, P. K. and C. R. Johnson. 1998. Spatio-temporal variation in coral recruitment at different scales on Heron reef, southern Great Barrier Reef. *Coral Reefs* 17:71-81.

Fabricius, K. E. and E. Wolanski. 2000. Rapid smothering of coral reef organisms by muddy marine snow. *Estuar. Coast. Shelf Sci*. 50: 115-20.

Fisk, D.A., and V.J. Harriott. 1990. Spatial and temporal variation in coral recruitment on the Great Barrier Reef: implications for dispersal hypotheses. *Mar. Biol.* 107, 485-490.

Franklin, H., Muhando, C.A., and U. Lindahl. 1998. Coral culturing and temporal recruitment patterns in Zanzibar, Tanzania. *Ambio* 27, 651-655.

GEPA. 1998. *1998 Microbiological Analysis of Guam's Recreational Marine Waters.* Report prepared by the Recreation Beach Monitoring Program, Guam Environmental Protection Agency. 56 pp.

Gilmour, J. 1999. Experimental investigation into the effects of suspended sediment on fertilization, larval survival and settlement in a scleractinian coral. *Mar. Biol.* 135: 451-62.

Gleason, M.G., 1996. Coral recruitment in Moorea, French Polynesia: the importance of patch type and temporal variation. *J. Exp. Mar. Biol. Ecol.* 207: 79-101.

Harii, S., H. Kayanne, H. Takigawa, T. Hayashibara, and M. Tamamoto. 2002. Larval survivorship, competency periods and settlement of two brooding corals, *Heliopora coerulea* and *Pocillopora damicornis*. *Mar. Biol.* 141: 39-46

Harriott, V. J. 1985. Recruitment patterns of scleractinian corals at Lizard Island, Great Barrier Reef. *Proc 4th Int. Coral Reef Symp.* 4: 367-72.

Harriott V.J. & D.A. Fisk 1987. A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. *Mar. Ecol. Prog. Ser.* 37:201-208

Harrison, R. L. and C. C. Wallace. 1990. Reproduction, dispersal and recruitment of scleractinian corals. In *Ecosystems of the World 25: Coral Reefs* (Z. Dubinsky, ed.). Elsevier. Amsterdam. Pp 133-207.

Hodgson, G. 1990. Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. *Coral Reefs*. 9(1): 41-3.

Hughes T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, B. L Willis.1 999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59-63

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity and larval recruits. *Ecology* 81: 2241-9.

Hunte, W. and M. Wittenberg. 1992. Effects of eutrophication and sedimentation on juvenile corals. *Mar. Biol.* 114: 625-31.

Kojis, B.L. and N. J. Quinn. 1994. Seasonal and depth variation in fecundity of Acropora palifera at two reefs in Papua New Guinea. *Coral Reefs* 3:165-172.

Kojis, B.L., Quinn, N.J., 2001. The importance of regional differences in hard coral recruitment rates for determining the need for coral restoration. *Bull. Mar. Sci.* 69, 967-74.

Koop, K, D. Booth, A. Broadbent, J. Brodier, D. Bucher, D. Capone, J. Coll, W. Dennison, M. Erdmann, P. Harrison, O. Hoegh-Guldberg, P. Hutchings, G. B. Jones, A. W. D. Larkum, J. O'Neil, A. Steven, B. Tentoreis, S. Ward, J. Williamson, and D. Yellowlees. 2001. ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Mar. Poll. Bull.* 42: 91-120.

Kuffner, I. 2001. Effects of ultraviolet radiation (UV) on larval settlement of the reef coral *Pocillopora damicornis*. *Mar. Ecol. Prog. Ser.* 217:251-61.

Lundgren, I. and D. Minton. 2005. Is coral recruitment limited by sedimentation at War in the Pacific National Historical Park? *War in the Pacific NHP Technical Paper Series #2.* 5 pp.

Maida, M., J. C. Coll, and P. W. Sammarco. 1994. Shedding light on scleractinian coral recruitment. *J. Exp. Mar. Biol. Ecol.* 180: 189-202.

McClanahan, T. R. and D. Obura. 1997. Sedimentation effects on shallow coral communities in Kenya. *J. Exp. Mar. Biol. Ecol.* 209:103-22.

Minton, D. 2005. Fire, erosion, and sedimentation in the Asan-Piti watershed and War in the Pacific NHP, Guam. Report prepared for the National Park Service. 99 pp.

Minton, D., I. Lundgren, A. Pakenham, D. Drake, and H. Tupper. 2005. Spatial and temporal patterns in sediment collection rates on coral reefs at War in the Pacific NHP, Territory of Guam. *War in the Pacific NHP Technical Paper Series #1*. 7 pp.

Mundy, C. N. and R. C. Babcock. Role of light intensity and spectral quality in coral settlement: Implications for depth-dependent settlement? *J. Exp. Mar. Biol. Ecol.* 223: 235-55.

Neudecker, S. 1981. Effects of substratum orientation, depth, and time on coral recruitment at Guam. [Abstract]. *Proc. 4th Int. Coral Reef Symp.* 1: 376.

NRCS. 1996. *Ugam Watershed Management Plan Territory of Guam.* USDA, NRCS, Pacific Basin Area, Agana Guam.

Nzali, L.M., Johnstone, R.W., Mgaya, Y.D., 1998. Factors affecting scleractinian coral recruitment on a nearshore reef in Tanzania. *Ambio* 27, 717-722.

Porter, V., T. Leberer, M. Gawel, J. Guiterrez, D. Burdick, V. Torres, and E. Lujan. 2005. The state of coral ecosystems of Guam. In *Status of Coral Reef Ecosystems of the United States and the Pacific Freely Associated States 2005* (J. Waddell, ed.). NOAA Technical Memorandum NOS NCCOS 11. NOA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team. Silver Springs, MD. Pp. 442-87.

Reyes, M. Z. and H. T. Yap. 2001. Effect of artificial substratum material and resident adults on coral settlement patterns at Dunjugan Island, Philippines. *Bull. Mar. Sci.* 69:559-566.

Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Mar. Ecol Prog. Ser.* 62: 185-202.

Rogers , C. S., H. C. Fitz III, M. Gilnack, J. Beets, and J. Hardin. 1984. Scleractinian coral recruitment patterns at Salt River Submarine Canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs* 3: 69-76.

Richmond, R. H. 1987. Energetics, competency, and long-distance dispersal of planual of the coral *Pocillopora damicornis*. *Mar. Biol.* 93: 527-33.

Richmond, R. H. 1993. Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. *Amer. Zool.* 33:524–536.

Richmond, R. H. 1997. Reproduction and recruitment in corals: critical links in the persistence of reefs. In *The Life and Death of Coral Reef* (C. E. Birkeland, ed.). Chapman and Hall, New York. Pp. 175-97

Richmond, R. H. and C. L. Hunter. 1990. Reproduction and recruitment of corals: comparisons among Caribbean, the tropical Pacific, and the Red Sea. *Mar. Ecol. Prog. Ser.* 60: 185-203.

Riegl, B. and G. M. Branch. 1995. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *J. Exp. Mar. Biol. Ecol.* 186: 259-75.

Rylaarsdam, K.W. 1983. Life histories and abundance patterns of colonial corals on Jamaican reefs. *Mar. Ecol. Prog. Ser.* 13, 249-60.

Sale, P. F. 1999. Recruitment in space and time. *Nature* 397:25-6

Sammarco, P. W. 1991. Geographically specific recruitment and postsettlement mortality as influences on coral communities: the cross-continental shelf transplant experiment. *Limnol. Oceaogr.* 36: 496-514.

Sato, M. Mortality and growth of juvenile coral *Pocillopora damicornis* (Linnaeus). *Coral Reefs* 4: 27-33.

Smith, S. R. 1997. Patterns of coral settlement, recruitment and juvenile mortality with depth at Conch Reef, Florida. *Proc. 8th Int. Coral Reef Symp.* 2: 1197-1202.

Sokal, R. R. and F. J. Rohlf. 1995. *Biometry* (3rd Edition). W.H. Freeman and Company. New York, NY. 887 pp.

Tomascik, T. 1991. Settlement patterns of Caribbean scleractinian corals on artificial along an eutrophication gradient, Barbados, West Indies. *Mar. Ecol. Prog. Ser.* 77:261-9.

U. S. Census Bureau. 2001. Census 2000 data for Guam. U.S. Census Bureau, Washington D.C.

Vermeij, M. J. A. In Press. Early life-history dynamics of Caribbean coral species on artificial substratum: the importance of composition, growth and variation in life-history strategy. *Coral Reefs.*

Wallace, C. C. 1985. Seasonal peaks and annual fluctuations in the recruitment of juvenile scleractinian corals. *Mar. Ecol. Prog. Ser.* 21: 289-98.

Ward S. and P. Harrison. 1997. The effects of elevated nutrient levels on settlement of coral larvae during the ENCORE experiment; Great Barrier Reef, Australia. *Proc 8th Int. Coral Reef Symp.* 1:891-6.

Ward S. and P. Harrison. 2000. Changes in gametogensis and fecundity of acroporid corals that were exposed to elevated nitrogen and phosphorous during the ENCORE experiment. *J. Exp Biol Ecol.* 246: 179-221.

Wilkinson, C. 2004. Executive Summary. In *Status of the Coral Reefs of the World: 2004* (C. Wilkinson ed.). Australian Institute of Marine Science. Pp. 7-50.

Wolansiki, E., R. H. Richmond, G. Davis, and V. Bonito. 2003. Water and fine sediment dynamics in transient river plumes in a small, reef-fringed bay, Guam. *Est. Coast. Shelf Sci.* 56: 1-13.

Wolansiki, E., R. H. Richmond, G. Davis, E. Deleersnijder, and R. R. Leben. 2003. Eddies around Guam, and island in the Mariana Islands group. *Contin. Shelf Sci.* 23: 991-1003.

Appendix A. Raw Data

Coral recruit counts, identities (Pocil=Pocilloporidae; Porit=Poritidae; Acrop=Acroporidae), and sediment collection at each study site for all four replicates. Site locations correspond to those in Figure 1. Coral recruit identifications are based on Babcock et al. 2003. Total sediments were derived by averaging the sediments collected in two PVC tubes. Collection rate (g/cm^2/day) were computed by dividing the total sediments collected by the circular area of the tube opening and the number of days the replicate was deployed.

Replicate 1 (Oct. 2004 – Jan. 2005)

Location	Recruits	Identity	Total Sediment (g)	Collection Rate (g/cm²/day)
C20			6.5517	0.0039
D20	1	Pocil	9.2400	0.0056
K20	1	Pocil	5.4859	0.0037
L20			12.4621	0.0077
O20	1	Pocil	298.8419	0.1686
P20			68.4860	0.0386
Q20			11.6268	0.0068
R20			17.2251	0.0101
Total Recruits	3			

Replicate 2 (Jan. – Apr. 2005)

Location	Recruits	Identity	Total Sediment (g)	Collection Rate (g/cm²/day)
C20			5.5102	0.0038
D20	1	Pocil	12.8738	0.0091
K20			5.8981	0.0039
L20	2	Pocil, Pocil	37.1039	0.0256
O20	1	Pocil	335.0596	0.2345
P20			108.0099	0.0746
Q20			18.1087	0.0132
R20			6.8053	0.0050
Total Recruits	4			

Replicate 3 (Apr. – Jun. 2005)

Location	Recruits	Identity	Total Sediment (g)	Collection Rate (g/cm²/day)
C20	1	Porites	No data	No data
D20	1	Porites	1.6745	0.0011
K20			1.2575	0.0008
L20			1.8396	0.0012
O20			10.7009	0.0069
P20			3.9878	0.0025
Q20			1.7821	0.0011
R20			1.2567	0.0008
Total Recruits	2			

Replicate 4 (Jun. – Sep. 2005)

Location	Recruits	Identity	Total Sediment (g)	Collection Rate (g/cm²/day)
C20			1.9951	0.0012
D20	1	Pocil	8.0228	0.0047
K20	2	Porit, Pocil	4.8261	0.0028
L20			15.4781	0.0091
O20			81.1003	0.0482
P20	3	Porit, Porit, Acrop	16.3189	0.0097
Q20	1	Pocil	49.6420	0.0298
R20			4.3433	0.0026
Total Recruits	7			

Appendix B. Individual Recruit Data

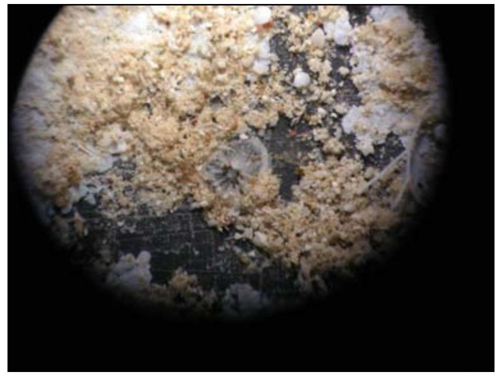
Raw data for each coral recruit, including a recruit ID, identity of the recruit (family or genera, if known), replicate (1-4), plate (T=top, B=bottom) and plate surface (U=upper, L=lower) on which the recruit was found, the size (number of polyps) as determined from the photographs, and the distance (mm) of the recruit from the edge of the plate. Recruit ID correspond to the photographs in Appendix C.

Recruit ID	Identity	Replicate	Plate	Surface	Size (# of polyps)	Distance (mm)
1-D20	Pocilloporidae	1	B	U	1	4
1-K20	Pocilloporidae	1	T	U	1	11
1-O20	Pocilloporidae	1	T	U	12	32
2-D20	Pocilloporidae	2	T	U	1	3
2-L20a	Pocilloporidae	2	B	U	7	2
2-L20b	Pocilloporidae	2	B	U	12	4
2-O20	Pocilloporidae	2	T	U	10	39
3-C20	Poritidae	3	T	U	1	12
3-D20	Poritidae	3	B	L	1	11
4D-20	Pocilloporidae	4	T	U	12	1
4-K20a	Poritidae	4	B	U	1	49
4-K20b	Pocilloporidae	4	T	U	7	4
4-P20a	Poritidae	4	T	U	1	36
4-P20b	Poritidae	4	T	U	1	44
4-P20c	Acroporidae	4	T	U	1	42
4-Q20	Pocilloporidae	4	T	U	6	11

Appendix C. Recruit Photographs

All high-resolution digital photographs of each recruit were taken using a dissecting microscope fitted with a MaxView Plus adapter set and Olympus 5050 digital camera. Recruit ID corresponds with those in Appendix B.

Recruit 1-D20 (Pocilloporidae)



Recruit 1-K20 (Pocilloporidae)

Recruit 1-O20 (Pocilloporidae)

Recruit 2-D20 (Pocilloporidae)

Recruit 2-L60a (Pocilloporidae)

Recruit 2-L60b (Pocilloporidae)

Recruit 2-O20 (Pocilloporidae)

Recruit 3-C20 (Poritidae)

Recruit 3-D20 (Pocilloporidae)

Recruit 4-D20 (Pocilloporidae)

Recruit 4-K20a (Poritidae)

Recruit 4-K20b (Pocilloporidae)

Recruit 4-P20a (Poritidae)

Recruit 4-P20b (Poritidae)

Recruit 4-P20c (Acroporidae)

Recruit 4-Q20 (Pocilloporidae)